THE SYSTEMATICS AND DISTRIBUTION OF MARINE TUBIFICIDAE (ANNELIDA: OLIGOCHAETA) IN THE BAHIA DE SAN QUINTIN, BAJA CALIFORNIA, WITH DESCRIPTIONS OF FIVE NEW SPECIES

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ABSTRACT: Marine Tubificidae (Annelida, Oligochaeta) from Bahia de San Quintin, Baja California, are described, and their distribution in the bay noted relative to the mean particle size of the sediments. *Tubifex postcapillatus*, n. sp. is characterized by its simple-pointed dorsal setae, and short hair setae which occur in postclitellar segments only. The setal pattern and details of the genital anatomy distinguish *Thalassodrilus belli*, n. sp. from other members of its genus. Both of these species are associated with the finest sediments which are located mainly at the north end of the bay. *Limnodriloides monothecus*, n. sp. with its single, mid-dorsal spermatheca unique to this genus, occurs mainly in silts and very fine sands (4 to 5 ϕ). *Limnodriloides verrucosus*, n. sp. possesses a papillate body wall previously unknown in the genus, but reminiscent of the *Peloscolex* condition; it occurs in all sediment types in the bay (3 to 8 ϕ) but is most abundant in the 5 to 6 ϕ range. The dominant oligochaete, *Limnodriloides barnardi*, n. sp., closely resembles *Limnodriloides winckelmanni* Michaelsen, especially in its possession of elongate, grooved spermathecal setae enclosed in vacuolated sacs; the species are distinguished by details of their penial structures. *Limnodriloides barnardi*, n. sp. occurs in all sediment classes but its optimum range appears to be in 4 to 6 ϕ sediments.

In a general report on the benthic exploration of Bahia de San Quintin, Baja California, in 1960–1961, Barnard (1962) pointed out that unpolluted or unmodified bays and enclosures of the Southern Pacific region of North America are both rare and poorly known biologically. Barnard (op. cit.) states the two primary objectives of the survey as ". . . a search for basic information on an unpolluted enclosure as near southern California as possible, and the initiation of comparative investigations planned by the Institute of Marine Bio-Research on many such enclosures in the Eastern Pacific." This paper reports on the systematics and distribution within Bahia de San Quintin of the tubificid oligochaetes.

The recognition of Oligochaeta, mainly Tubificidae, as regular components of the marine benthic community, has occurred only within the last decade. Previously oligochaetes were regarded as more or less exclusively fresh-water or terrestrial with an occasional species "invading" the marine environment via estuaries and fresh-water sources in the littoral zone. Undoubtedly this may be true of some species, but the works of Brinkhurst (1963; 1966), Hrabĕ (1966; 1967; 1971a; 1971b), and Cook (1969; 1970a; 1971) have demonstrated that a significant number of truly marine Tubificidae exist, including some from the deep sea (Cook, 1970b).

The collection of Tubificidae from Bahia de San Quintin, numbering 55 samples, each containing from 1 to about 500 worms, was received for examination from the Smithsonian Institution. Five species of Tubificidae have been recognized, namely, *Tubifex postcapillatus* n. sp., *Thalassodrilus belli* n. sp., *Limnodriloides barnardi* n. sp., *Limnodriloides monothecus* n. sp., and *Limnodriloides verrucosus* n. sp.

STUDY AREA AND METHODS

Bahia de San Quintin is located on the Pacific side of Baja California with its northeastern tip at 30° 30' N, 116° 00' W. A full description of the study area, field, and laboratory methods, involved in the survey is available in Barnard (1962). Briefly, an area of six square miles in the eastern arm of the bay was sampled as uniformly as possible at a density of 15 stations per square mile. A benthic sample was collected at each station (designated SQ 1 to 94) using a

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modified Hayward orange-peel grab with a capacity of 650 sq cm (0.065 sq cm). Material from the grab was washed through a Tyler screen (12.6 mesh strands per cm; mesh diameter 0.495 mm), the animals preserved in 4 percent formalin and transported to the laboratory. Here they were rewashed through a screen (23.6 mesh strands per cm), sorted into taxonomic groups, stored in formalin for three months and finally transferred to 70 percent ethanol.

The Oligochaeta had been lightly stained in eosin, dehydrated, and transferred to methyl salicylate by the late A. W. Bell, who had also made microscope slide preparations of one to four individuals from a number of samples; from this preliminary survey Bell had apparently recognized the presence of a *Limnodriloides* (some slides labelled as "*L. winckelmanni*") and a species of "*Peloscolex*" or "*Tubifex*" (= *T. post-capillatus*). After Bell's slides had been examined to assess the number and type of taxa involved, material in fluid was studied and identified using: a) temporary mounts in methyl salicylate; b) permanent whole mounts in Canada Balsam, stained in eosin; c) permanent mounts of dissected worms lightly stained in either eosin or Harris' haematoxylin. In 25 samples the numbers of worms were too large to permit identification of every individual, therefore subsamples of about 30 worms were taken by the following method which eliminates, or minimizes, any selection bias for large individuals. Material was transferred to a small dish where it was spread out uniformly (as estimated visually): 30 individuals were separated from one small area (size dependent on total sample size) and these identified. A rough estimate of the total number of individuals (T) in these samples was arrived at by comparing the area occupied by 30 individuals (As) with the total area of the sample dish (At); *i.e.*, $T = 30 (At)/As$.

SYSTEMATIC ACCOUNTS

Tubifex postcapillatus, new species

Figure 1

Holotype.—United States National Museum (USNM) catalogue number 45289. Bahia de San Quintin, Station number SQ 1. Depth, less than 2 m, in gray clay. Collected 22 April 1960.

Paratypes.—USNM 45290. Five individuals from SQ 9 (less than 2 m depth, in black sandy silt with small amounts of clay; collected 22 April 1960), and four individuals from SQ 5 (less than 2 m depth,

in dark grey silt collected 22 April 19.. Museum of Natural Science Ottawa On... catalogue number 3475. One individual d... holotype.

Etymology.—"*capillatus*" L. "long hair... hair"; hence species has hair setae posteriorly.

Description.—Up to 58 segments. About 1. mm long. Diameter 0.24 to 0.41 mm anteriorly, 0.? mm at segment XI, 0.33 mm tapering to a minimum of 0.16 mm posteriorly. Prostomium rounded as long as, or shorter than it is wide at the peristomium junction. Clitellum weakly developed on segments XI and ½ XII. Dorsal setae: in segments II to X each bundle contains 3 to 4, sometimes 5, bifid setae 75 to 85 μ long, with the upper tooth slightly longer than the lower; from about segment XIII to terminal segment each bundle contains two or three smooth hair setae 110 to 125 μ long, and two or three elongate, single-pointed crochets 80 to 95 μ long; modified crochets and hair setae are similar in appearance but differ in the latter's lack of a node, more slender form, and greater length. Ventral setae: anteriorly each bundle contains three to five bifid setae 70 to 88 μ long, with the upper tooth slightly longer than the lower; posteriorly each bundle has two setae similar in form and length to anterior setae. No modified genital setae. Paired spermathecal and male pores are situated in the line of the ventral setae on segments X and XI respectively.

Male genital system (all structures paired): vas deferens 25 to 31 μ diameter, about 1.25 mm long (in holotype), joins the atrium subapically and dorsally, opposite to the prostate gland. Atria hook—to commar-shaped, reflexed posteriorly, about 340 μ in total length, 54 to 100 μ diameter; atria reach their maximum diameter distally to vas deferens prostate junctions; internal lining epithelium of this swelling more glandular than remaining atrial lining. Atria terminate in cuticularized penes 105 to 135 μ long, 50 to 70 μ diameter. Prostate gland relatively small, more or less enclosed by "hook" of atrium. Paired spermathecae with large ovoid to sacciform ampullae and barrel-shaped ducts about 135 μ long, 60 μ diameter. Spermatozeugmata elongated ovoids, about 260 μ long, 63 μ maximum diameter.

Remarks.—*Tubifex postcapillatus* differs from other members of the genus in possessing hair setae and simple-pointed crochets only in posterior segments. In other species, where they occur, hair setae are always present in, and tend to be more numerous on, anterior segments. Simple-pointed posterior setae are known in some *Peloscolex* species [*e.g.*, *P. heterochaetus* (Michaelsen, 1926), *P. swirencovi* (Jaroshenko, 1948) and *P. intermedius* Cook, 1969] but this genus is characterized by the possession of a papillate or ridged body wall, at least at some time in its life cycle; the distinctions between *Tubifex* and
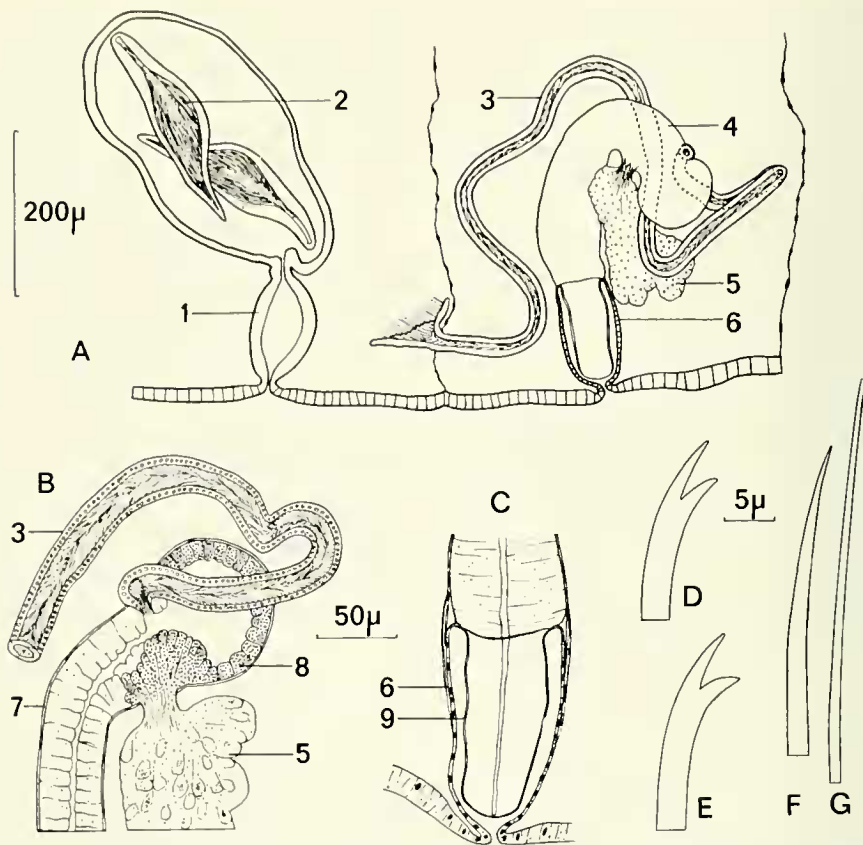
Figure 1. *Tubifex postcapillatus*, n. sp. A, Longitudinal view of genital segments; B, Distal end of atrium (optical section); C, Penis; D, Anterior dorsal seta; E, Anterior ventral seta; F, Posterior dorsal crochet; G, Part of hair seta (same bundle as F). 1, spermathecal duct; 2, spermatozeugma; 3, vas deferens; 4, atrial ampulla; 5, prostate gland; 6, penial sac; 7, atrial muscle layer; 8, glandular epithelium of distal atrium; 9, penial sheath.

Peloscolex, which are complex and probably artificial, are discussed in Pickavance and Cook (1971). Immature, semi-mature and mature individuals of *T. postcapillatus* which were examined showed no trace of papillation, body wall ridges or accumulations of foreign particles, and is therefore precluded from *Peloscolex* as this is presently defined.

Thalassodrilus Brinkhurst, 1963

Definition.—Hair setae absent. Penial setae present or absent. Body wall smooth. No gut diverticulae. Thick muscle layer associated with paired atria, at least terminally. Wide vasa deferentia, shorter than, or about as long as the atria, enter the latter apically. Each atrium with a small compact prostate gland. Spermathecae small or absent. Sperm in spermathecae in random masses; spermatozeugmata absent. Coelomocytes absent.

Type species.—*Rhyacodrilus prostatus* Knöllner, 1935.

Remarks.—*Thalassodrilus* was established by Brinkhurst (1963) to accommodate *R. prostatus*. Hrabě (1967) rejected the genus and placed *R. prostatus* in *Limnodriloides* but later (Hrabě, 1971b) modified his opinion, redefined *Thalassodrilus*, and included in it *R. prostatus*, *Limnodriloides roseus* Pierantoni, 1903, *Limnodriloides pectinatus* Pierantoni, 1903, and *Limnodriloides gurwitschi* Hrabě, 1971 (1971a). The modified definition of *Thalassodrilus* given above differs from Brinkhurst's (1963) and Hrabě's (1971b) conception of the genus by its specific reference to the heavy musculature associated with the male genitalia, and contains *T. prostatus* (Knöllner), *T. gurwitschi* (Hrabě) and *T. belli*, n. sp. The descriptions of *L. roseus* and *L. pectinatus* are in-

adequate and in this author's opinion should remain as species inquirendae in *Spiridion* (Cook, 1969; Brinkhurst and Jamieson, 1971); they cannot be included in either *Limnodriloides* because they lack gut diverticulae, or *Thalassodrilus* because they do not possess heavy atrial or pseudopenial musculature.

Some problems with *Thalassodrilus* do remain however. *Thalassodrilus gurwitschi* and *T. belli* are clearly closely related and, except for their lack of gut diverticulae and possession of relatively wide vasa deferentia, could be considered as species of *Limnodriloides*; both differ from *T. prostatus* in their common possession of thick muscular pseudopenes and distinct thin-walled atria, rather than the thick, muscular, pear-shaped structures thought to be the atria in *T. prostatus*. It is argued that the latter could be derived from a *T. gurwitschi*-like ancestor by the excessive or precocious development of the pseudopenial musculature which finally enveloped and incorporated the original atrium both morphologically and functionally. The author feels that because of this possible mechanism together with the possession of relatively wide vasa deferentia and the other, mainly negative, characters included in the generic definition, the three species here included in *Thalassodrilus* form a convenient, and possibly monophyletic group. An additional advantage of the arrangement is the removal of *T. gurwitschi* (and *T. belli*) from *Limnodriloides* which therefore remains the homogenous taxon defined in Cook (1969) (and see discussion under *Limnodriloides*, below).

KEY TO SPECIES OF *THALASSODRILUS*

1a. Penial setae present. Atria pear-shaped with thick muscular walls .... *T. prostatus* (Knöllner)
b. Penial setae absent. Atria elongate, thin-walled, with muscular pseudopenes terminally 2
2a. Spermathecae present .... *T. belli*, n. sp.
b. Spermathecae absent .... *T. gurwitschi* (Hrabě)

Thalassodrilus belli, new species

Figure 2

Holotype.—USNM 45287. Bahia de San Quintin. Station SQ 3. Depth, less than 2 m, in gray clay. Collected 22 April 1960.

Paratypes.—USNM 45288. One individual from SQ 1 (in black mud); four individuals from SQ 2 (in dark gray clay); one individual from SQ 6 (very dark clay, some lighter clay); one individual from SQ 7 (black sandy silt); for all stations depth,

less than 2 m; collected 22 April 1960 ....
One individual from SQ 5. Depth, less than [...] dark gray silt. Collected 22 April 1960.

Etymology.— The species is named in [...] of the late Dr. A. W. Bell, who began to c[...] part of this collection.

Description.—55 to 63 segments. 13 to 17 mm long. 0.32 to 0.43 mm diameter anteriorly, 0.42 to 0.61 mm at segment XI, 0.4 mm tapering to 0.2 mm posteriorly. Prostomium shorter than it is wide at the peristomium junction. Clitellum restricted to segment XI and a small part of segment XII. Dorsal and ventral setae similar in number, size and shape; setae three to five per bundle anteriorly, two per bundle posteriorly; setae bifid, 69 to 105 μ long, with the upper tooth slightly thinner than, but as long as, the lower; setae in the middle region of the body tend to be shorter than others. Paired male and spermathecal pores open in the line of the ventral setae; spermathecal pores open near intersegmental furrow IX X.

Pharyngeal glands in segments IV and V. Chloragogen cells begin in segment VI. No discernable gut diverticulae. Male genital system (all structures paired): vas deferens, about 265 μ long, 20 to 30 μ diameter, joins atrium apically. Atrium about 335 μ long, with an apical swelling 47 to 54 μ diameter, and a long duct 20 to 26 μ diameter which is convoluted or folded proximally. Folded part is enclosed in a muscular sac, forming a protrusible pseudopenis. Prostate gland small, joined to the atrial swelling ventrally. Paired spermathecae relatively very small, pear-shaped. 70 to 110 μ diameter with very short, indistinctly separated ducts. Sperm in spermathecae in random masses.

Remarks.—The general dimensions, the peculiar form of the male genitalia, the number and form of the setae, and the absence of gut diverticulae, are all characters similar in, or common to, both *T. belli* and *T. gurwitschi*. The latter species, however, has no trace of spermathecae in the many mature and immature individuals studied by Hrabě (1971a: pers. comm.). A further distinction between the two species is found in the setae; in *T. gurwitschi* the upper tooth of each seta is distinctly thinner at the base than the lower tooth (Hrabè. 1971a. Fig. 1 a–c) whereas in *T. belli* the basal width of the teeth are approximately equal (Fig. 2d).

Limnodriloides Pierantoni, 1903

Definition.—Hair setae absent; somatic setae all bifid crochets. Penial setae absent. Body wall smooth or, rarely, with raised papillae. Gut in immediate preclitellar region with a pair of diverticulae. Paired atria divisible into well-defined ampullar and duct regions, both with relatively thin muscle walls. Vasa
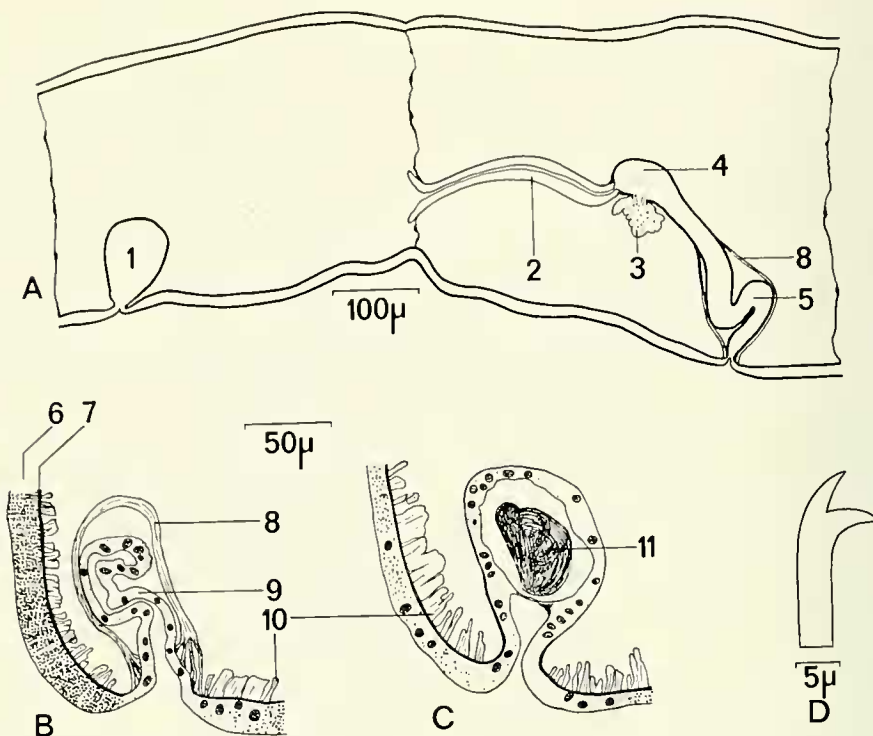
Figure 2. *Thalassodrilus belli,* n. sp. A, Longitudinal view of genital segments; B, Transverse section of male pore; C, Transverse section of spermatheca; D, Seta (segment VIII). 1, spermatheca; 2, vas deferens; 3, prostate gland; 4, atrial ampulla; 5, penial complex; 6, epithelium of clitellum; 7, circular muscle; 8, muscle sac surrounding penis; 9, lining epithelium of penial duct; 10, longitudinal muscle; 11, sperm mass.

deferentia about as long as, or slightly longer than, the atrial ampullae (excluding the duct) which they join more or less apically. Compact prostate glands join atria on discrete, broad prostatic ducts. Penial structures variable in form but are rarely absent. Spermathecae relatively large. Spermatozeugmata absent, but in most species sperm in the spermathecae are organized into discrete, oriented bundles. Coelomocytes absent.

Type species.—*Limnodriloides appendiculatus* Pierantoni, 1903.

Remarks.—A short history of *Limnodriloides,* a revised diagnosis of the genus, and reasons for removing *S. rosens* (Pierantoni) and *S. pectinatus* (Pierantoni) from it, are given in Cook (1969) (also *vide supra* under *Thalassodrilus*). Briefly, the presence of the unique gut diverticulae found in the eighth or ninth segment is considered as the positive unifying somatic character of *Limnodriloides.* Hrabě (1971b) apparently accepted this proposition but, on the basis of the structure of the intromittent organs, split the genus into two; he restricted *Limnodriloides* to

those species possessing pseudopenes (containing *L. appendiculatus, L. agnes,* Hrabě, 1967, and *L. winckelmanni* Michaelsen, 1914) and established *Bohadschia* for the species with true penes (containing *L. medioporus* Cook, 1969, *B. maslinicensis* Hrabě, 1971, and *B. pierantonii* Hrabě, 1971). In this paper three new species are described; *L. monothecus* and *L. verrucosus* which both possess pseudopenes (*i.e. Limnodriloides sensu* Hrabě) and *L. barnardi* which has complex intromittent organs showing characteristics of both pseudopenes and true penes (see remarks following the description of this species). Because of this intermediate type and because *L. barnardi* appears to be very close to *L. winckelmanni,* the distinction between Hrabě's *Limnodriloides* and *Bohadschia* can no longer be considered valid, even at the subgeneric level, therefore Cook's (1969) conception of *Limnodriloides* is retained in this account.

Limnodriloides monothecus is analogous to *P. monospermathecus* (Knöllner, 1935) in *Phallodrilus;* in both cases the possession of a single

dorsal spermatheca, rather than paired ventral ones, is considered to be significant at the species level only. However, the organization of the sperm in the spermatheca of *L. monothecus*, and other members of the genus, needs closer examination.

In *L. appendiculatus*, *L. agnes*, and *L. medioporus*, the sperm is arranged in the spermathecae in oriented bundles (Hrabě, 1967; Cook, 1969); in *L. winckelmanni* and *L. barnardi* the sperm bundles are more regular in form than those of the three former species (Michaelsen, 1914; Hrabě, 1967; *vide infra*); both Michaelsen and Hrabě (op. cit.) refer to these structures as spermatophores or spermatozeugmata in *L. winckelmanni*, and Hrabě (1967) is unable to decide whether the sperm bundles of *L. agnes* are spermatozeugmata or not. Observation of the sperm bundles of *L. medioporus* and *L. barnardi* has shown that the sperm tails tend to be organized into parallel bundles, some of which appear to have coalesced or adhered closely to each other. The orientation of sperm is developed to a higher degree in *L. monothecus*; in this species the sperm bundles are very long and narrow with the sperm heads (darkly staining in haematoxylin) concentrated at one end of the bundle, and the sperm tails, arranged in very loose spirals, composing the remaining two-thirds of the bundle (Fig. 4b). The term "spermatozeugma" is used in the Tubificidae to denote a sperm aggregation in which sperm heads occur around a central axis with the sperm tails, which are embedded in a cementing substance, radiating from this axis in a spiral manner (Stephenson, 1930; Brinkhurst and Jamieson, 1971). The sperm bundles of *Limnodriloides*, including the highly organized bundles of *L. monothecus* cannot therefore be considered as spermatozeugmata.

A character which has been added to the generic diagnosis of *Limnodriloides* is the nature of the body wall. This is necessary because of the discovery of *L. verrucosus* which, although clearly a *Limnodriloides* (form of the male genitalia and presence of gut diverticulae) has a papillate body wall superficially indistinguishable from that of many species of *Peloscolex* (see also remarks following the description of *L. verrucosus*).

KEY TO SPECIES OF *LIMNODRILOIDES*

1a. One pair long, hollow-ended spermathecal setae, each contained in large muscle-coated sac, situated on segment X. Atrial duct lined, at least in part, with glandular epithelium 2

b. Modified spermathecal setae absent, without glandular lining epithelium

2a. Intromittent organs small pseudopenes surrounding ends of spermathecal setae thicker than setal shaft   *L. winckelmanni* Michaelsen.

b. Intromittent organs large penes (in part) enclosed in voluminous penial sacs. Muscle surrounding ends of spermathecal setae about as thick as setal shaft   *L. barnardi*, n. sp.

3a. Single, elongate, carrot-shaped spermatheca present, opening mid-dorsally   *L. monothecus*, n. sp.

b. Spermathecae paired, opening ventrally or ventro-laterally   4

4a. Body wall papillate, at least in postclitellar region
                                  L. verrucosus, n. sp.

b. Body wall smooth   5

5a. In posterior segments setae one per bundle. Atrial duct at least as long as vas deferens
                              L. agnes Hrabě.

b. In posterior segments setae two per bundle. Atrial duct shorter than vas deferens   6

6a. Genital pores contained in median ventral folds in body wall, appearing externally as elongate median slits arranged transversely
                         L. medioporus Cook.

b. Genital pores paired, ventro-lateral   7

7a. Gut diverticulae in segment VIII
                     L. appendiculatus Pierantoni.

b. Gut diverticulae in segment IX   8

8a. In preclitellar segments setae two per bundle. Vasa deferentia 9 to 13 μ wide. Terminal part of male ducts S-shaped
                        L. maslinicensis (Hrabě).

b. In preclitellar segments setae usually three per bundle. Vasa deferentia 16 μ wide. Terminal part of male ducts straight
                          L. pierantonii (Hrabě).

Limnodriloides monothecus, new species

Figure 3

Holotype.—USNM 45285. Bahia de San Quintin, station SQ 16. Depth, less than 2 m, in dark grey sandy silt. Collected 23 April 1960.

Paratypes.—USNM 45286. Six individuals, data as for holotype: one individual from SQ 3⁷ (Depth, less than 2 m, in grey silt, collected 24 April 1960). NMC 3478. One individual from SQ 9 (Depth, less than 2 m, in black sandy silt with small amounts of clay, collected 22 April 1960).

Etymology.—"mono" = Gr. "one, single"; "theca" = Gr. and L. "case, receptacle"; hence "single spermatheca."

Description.—About 46 segments, 9.5 mm long, 0.12 to 0.23 mm diameter anteriorly, 0.25 to 0.27 mm at segment XI, 0.23 tapering to 0.17 mm posteriorly. Prostomium rounded, shorter than it is wide at the peristomium junction. Clitellum very weakly developed or indiscernible. Dorsal and ven-
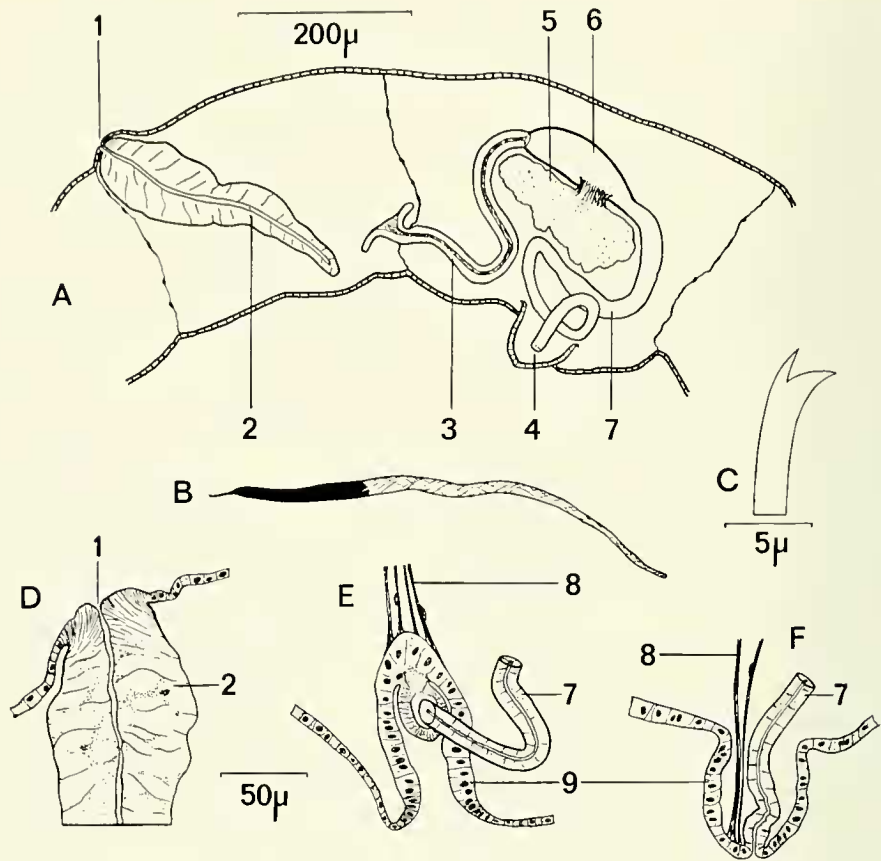
Figure 3. *Limnodriloides monothecus*, n. sp. A, Longitudinal view of genital segments; B, Sperm bundle; C, Somatic seta; D, Proximal end of spermatheca; E, Penis sac (resting position); F, Penis sac (everted position). 1, spermathecal pore; 2, spermatheca; 3, vas deferens; 4, male pore; 5, prostate gland; 6, atrial ampulla; 7, atrial duct; 8, penis rectractor muscles; 9, penis sac epithelium.

tral setae similar in number, size and shape: setae 3, sometimes two per bundle in segments II to IX, absent in X and XI, and two per bundle from segment XII to terminal segment; setae bifid, 40 to 50 μ long, with upper tooth shorter and thinner than the lower. No modified genital setae. A single mid-dorsal spermathecal pore is situated near intersegmental furrow IX/X. Male pores paired, ventrolateral.

Pharyngeal glands present in segments IV and V. A pair of diverticulae join the gut in the middle of segment IX. Male genital system (all structures paired): relatively thick vas deferens, 23 to 34 μ diameter, 245 to 300 μ long, joins atrium more or less apically. Atrium consists of an ovoid ampulla, 90 to 130 μ long, 35 to 50 μ diameter, and an elongate, tubular duct 450 to 550 μ long, 13 to 27 μ diameter, which opens to the exterior in an evaginable sac from the median side; sacs 90 to 105 μ long, 60 to 77 μ maximum diameter when evaginated. Prostate gland joins atrium ventrally, near to the ampulla

duct junction. Single median spermatheca elongate, carrot-shaped, 280 to 400 μ long, 55 to 85 μ maximum diameter, tapering to about 20 μ distally. Sperm in spermatheca oriented into long narrow bundles 200 to 260 μ long, 6.8 μ maximum diameter, with the darkly staining sperm heads all occurring at one end of the bundle.

Remarks.—The single, mid-dorsal spermatheca found in *L. monothecus*, though unique in *Limnodriloides*, is also known in *Phallodrilus monospermathecus*.

Limnodriloides verrucosus, new species

Figure 4

Holotype.—USNM 45283. Bahia de San Quintin, station SQ 41. Depth, less than 2 m, in gray very fine sandy silt. Collected 24 April 1960.
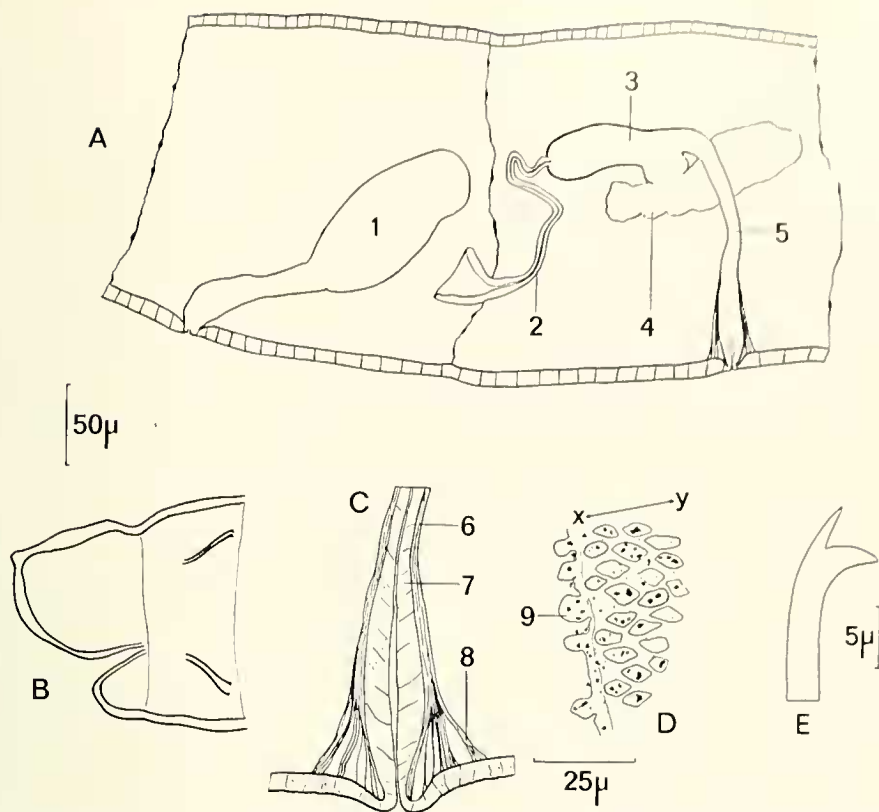
Figure 4. Limnodriloides verrucosus, n. sp. A, Longitudinal view of genital segments: B, Prostomium and first two segments; C. Penis; D, Body wall of posterior segment (x – y = transverse axis of body); E, Somatic seta. 1, spermathecal ampulla; 2, vas deferens; 3. atrial ampulla; 4, prostate gland; 5, atrial duct; 6, circular muscle layer of atrial duct; 7, atrial duct lining epithelium; 8, penis protractor muscle; 9, body wall papilla.

Paratypes.—USNM 45284. One individual from SQ 39 (in gray very fine sand; collected 23 April 1960); three individuals from SQ 46 (in gray silty very fine sand; collected 24 April 1960); two individuals from SQ 49 (in gray very fine silty sand; collected 24 April 1960); two individuals from SQ 58 (in gray silty very fine sand; collected 24 April 1960). NMC 3476. One individual from SQ 54 (in gray silty fine sand; collected 24 April 1960). Depths (all paratypes), less than 2 m.

Etymology.—"*verrucosus*" = L. "warty."

Description.—Up to 45 segments. 7.5 to 13 mm long. 0.12 to 0.18 mm diameter anteriorly, 0.18 to 0.25 mm at segment XI, 0.17 tapering to 0.08 mm posteriorly. Prostomium a little shorter than it is wide at the peristomium junction, with a small, thin-walled papilla anteriorly. Body wall covered with a sparse to very dense layer of raised papillae and small foreign particles, usually beginning just behind the clitellum in mature individuals, but occurring in anterior segments of immature specimens. Clitellum confined to segments XI and a small part of XII.

Dorsal and ventral setae similar in number, size and shape: setae two per bundle in segments II to VII and one per bundle from VIII to the terminal segment; setae absent on segments X and XI (no modified genital setae); all setae bifid, 40 to 65 μ long. with the upper tooth thinner than, but about as long as the lower. Male and spermathecal pores paired in the line of the ventral setae.

Pharyngeal glands in segments IV and V. A pair of diverticulae join the gut ventro-laterally in the middle region of segment IX and extend anteriad to septum VIII IX. Male genitalia (all structures paired): vas deferens, 7.3 to 10.5 μ diameter and about as long as, or slightly shorter than the atrium. join latter apically. Atrium thin. elongate, with a thickly stalked prostate gland joining its ampulla ventrally on a raised papilla. Atrium with a cylindrical ampulla about 100 μ long. 13.7 to 35 μ diameter, and a tubular duct 8 to 11.5 μ diameter swelling to about 21 μ terminally: total length of atrium about 220 μ. Long axis of atrium directed anteriorly. Muscles from swollen end of atrial duct join body

wall, forming a protrusible pseudopenis. Paired spermathecae with ovoid to elongate ampullae 97 to 113 μ long, 48 to 57 μ wide, and discrete ducts 57 to 73 μ long, 14 to 19 μ diameter. Sperm in spermathecae in random masses (no trace of oriented bundles).

Remarks.—The papillate body wall of *L. verrucosus* is unique in *Limnodriloides*, but is morphologically indistinguishable from the condition found in many *Peloscolex* species. In the latter genus wide intraspecific variation of the nature of the body wall is known: Dahl (1960) found that *Peloscolex benedeni* (Udekem) shed its cuticle and papillae at maturity, and Brinkhurst (1964) states that the freshwater *Peloscolex ferox* (Eisen) attains the papillate condition from a nonpapillate juvenile and then periodically, though not strictly seasonally, sheds its papillae. A study of 197 individuals of *L. verrucosus* in different states of maturity (Types and USNM 45292) has revealed the following variation pattern in its body wall: papillae are developed on segments IV or V to the terminal segment, prior to, or immediately after, emerging from the cocoon; the papillae grow with the animal and may also develop on the first few anterior segments; as the individual reaches sexual maturity there appears to be a progressive loss of papillae from the anterior end until the body wall is papillate only in the postclitellar region; after copulation and cocoon deposition, it appears that both the genitalia and the papillae regress, or the latter shed (as in *Peloscolex*).

The general body form and dimensions, the papillate body wall, and the number and form of the setae of *L. verrucosus* are strikingly similar to those of *Peloscolex gabriellae* Marcus, 1950. The latter appears to be a widespread, amphiamerican, marine species, or species complex, with very wide ecological tolerances (Cook, 1970b), and because its setal pattern is unique within *Peloscolex*, its presence is sometimes diagnosed on the basis of immature individuals. However, unless the gut diverticulum character, which is rarely checked in routine tubificid identifications, is examined, immature *P. gabriellae* and *L. verrucosus* can be mistaken for each other.

Limnodriloides barnardi, new species

Figure 5

Holotype.—USNM 48730. Bahia de San Quintin. station SQ 16. Depth, less than 2 m, in dark grey sandy silt. Collected 23 April 1960.

Paratypes.—USNM 48731. Two individuals, data as for holotype. Two individuals from SQ 8 (in black silt; collected 22 April 1960). One individual from each of SQ 19, 22, 30, 37, 46, 51, 85, 91; two individuals from SQ 15. NMC 3480. One individual from SQ 2. All paratypes collected April 1960 at a depth of less than 2 m.

Additional (non-type) material.—USNM 45291 and 45297.

Etymology.—Named for J. Laurens Barnard (Smithsonian Institution) who led the expedition to Bahia de San Quintin.

Description.—About 35 segments. 8 to 10 mm long. 0.12 to 0.20 mm in diameter anteriorly, 0.25 to 0.30 mm at clitellum, 0.10 to 0.16 mm posteriorly. Prostomium a little shorter than it is wide at the peristomium junction, with a small papilla anteriorly. Clitellum weakly developed on segments XI and XII. Dorsal and ventral setae similar in number, size and shape: somatic setae bifid, 40 to 60 μ long, with subequal teeth; in preclitellar region each setal bundle contains 3, sometimes two or four setae; posteriorly each bundle contains two setae. Each ventral bundle of segment X contains one slender, straight or curved, elongate spermathecal seta 110 to 120 μ long, which has a hollow groove from the node to the distal end; proximal end of spermathecal setae, on which the setal protractor muscles are inserted, are strongly hooked; distal half of spermathecal setae each enclosed in a pear-shaped sac, 65 to 70 μ long, 40 to 48 μ diameter, which consists of an inner layer of vacuolated cells and an outer muscle layer, and which connects with the body wall musculature. Ventral setae absent on segment XI. Paired male pores open in the line of the ventral setae on segment XI. Paired spermathecal pores open in the line of, or slightly lateral to the spermathecal setae (out of a total of 25 individuals examined for the character, 18 had spermathecal pores located anterior to the spermathecal setae, five had pores posterior to the setae, and two were without spermathecal setae).

Pharyngeal glands present in segments IV and V. Chloragogen cells begin in segment VI. Male genital system (all structures paired): conical male funnel situated ventrally on septum X/XI drains into the vas deferens, 9 to 12 μ diameter, about 180 μ long, which joins the atrium apically; atrium, whose long axis is directed anteriorly, consists of an ovoid to elongate ampulla, 100 to 110 μ long, 35 to 60 μ diameter, and an elongate duct, 95 to 135 μ long, 25 to 35 μ diameter, which terminates as the penis; a large, thickly-stalked prostate gland joins the atrial ampulla ventrally. Atrial ampulla consists of a thin outer muscle layer and an inner layer of thin lining cells. About the first 90 to 100 μ of the atrial duct (adjacent to the ampulla) is lined with thick, highly glandular cells. The penial complex consists of a more or less circular infolding of the body wall (the penial sac) 60 to 70 μ deep, 45 to 50 μ maximum
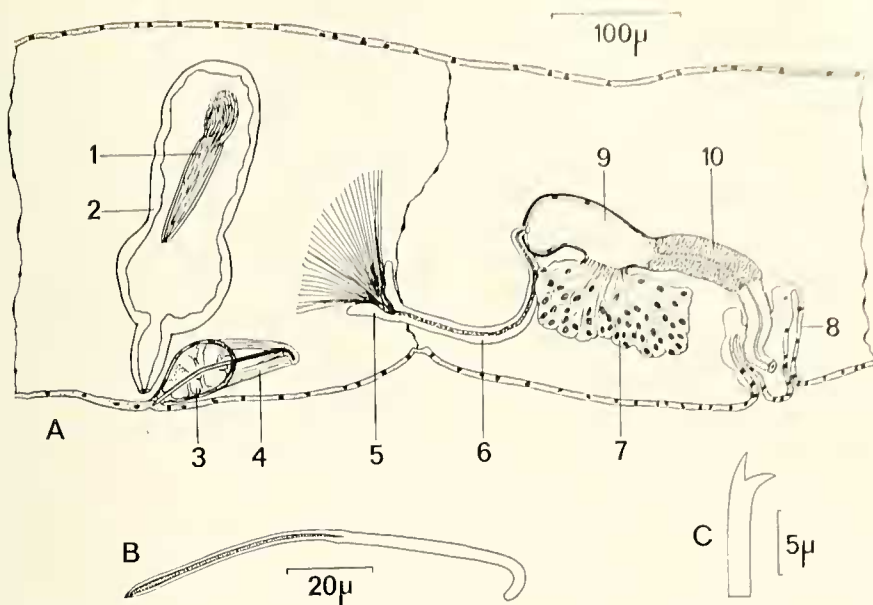
Figure 5. *Limnodriloides barnardi*, n. sp. A, Longitudinal view of genital segments; B, Spermathecal seta; C, Somatic seta. 1, sperm bundle; 2, spermathecal ampulla; 3, vacuolated muscular sac surrounding spermathecal seta; 4, protractor muscles of spermathecal seta; 5, male funnel; 6, vas deferens; 7, prostate gland; 8, penial sac; 9, atrial ampulla; 10, glandular part of atrial duct.

diameter, and a truncated-cone-shaped penis, through which penetrates the terminal part of the atrial duct; the latter opens on the penis subterminally and laterally. Paired spermathecae with discrete ducts 40 to 55 μ long, 30 to 35 μ maximum diameter, and elongate ampullae 200 to 220 μ long, 70 to 120 μ maximum diameter; latter tend to be constricted in the middle third of their length. Sperm in the spermathecae oriented into long narrow bundles, 95 to 135 μ long.

Remarks.—Morphologically, *L. barnardi* is very closely related to *L. winckelmanni*. Their atria and atrial ducts with glandular lining cells are, on available evidence, indistinguishable, and their spermathecal setae contained within vacuolated sacs are unique in the genus; the number and form of their setae are also similar. A comparison of the information available on *L. winckelmanni*, which is apparently derived from the type specimens alone (Michaelsen, 1914; Boldt, 1928; Hrabě, 1967; 1971b) with the description of *L. barnardi*, reveals that their intromittent organs differ (*vide infra*) and that the general dimensions of *L. barnardi* are smaller than those of *L. winckelmanni* (maximum body length, clitellum diameter and setal length of the two species are, respectively, 10 and 18 mm, 0.3 and 0.6 mm, 60

and 90 μ). The dimensions are probably not important characters as wide intra-specific variation in size is well known for many common tubificids and lumbriculids, but the different structures of their intromittent organs is more fundamental. Hrabě (1971b) showed that in *L. winckelmanni* small pseudopenial papillae cover the simple openings of the male ducts from the side. In *L. barnardi*, however, a large penial sac contains the terminal end of each atrial duct which opens subterminally on a truncated cone-shaped penis; employing present definitions of the terms, it would appear that the proximal part of this organ can be termed a true penis while the part distal to the actual male orifice could be considered as a pseudopenis.

ECOLOGICAL COMMENTS

The eastern arm of Bahia de San Quintin (referred to hereafter merely as "the bay") is a shallow body of water of more or less uniform salinity. At high tide the water depth over about 85 percent of the bay is less than two m; narrow, steep-sided channels (six to eight m deep) account for the remaining 15 percent (Barnard,

TABLE 1. Station data and number of tubificids in each bay sample. A—station number; B—fraction of sample counted and identified (S indicates subsamples of 30 worms); C—total number of tubificids, including immature specimens (numbers in brackets are estimated); D—mean particle diameter in μ; 1—*Tubifex postcapillatus*; 2—*Thalassodrilus belli*; 3—*L. monothecus*; 4—*L. verrucosus*; 5—*L. barnardi*.

A.	B.	C.	D.	1.	2.	3.	4.	5.
1	S	(130)	7	4	7	–	13	3
2	all	12	6	–	8	–	2	1
3	all	9	7	–	4	–	–	2
4	all	1	7	1	–	–	–	–
5	S	(300)	6	3	1	–	12	5
6	S	(75)	9	–	2	–	13	–
7	all	44	30	–	3	–	12	10
8	S	(200)	13	–	–	5	–	13
9	S	(100)	16	4	2	1	4	5
10	S	(200)	38	–	–	2	–	22
11	S	(150)	21	–	–	3	–	17
12	all	23	98	–	1	–	–	8
13	10%	4	26	–	–	–	–	2
14	S	(250)	56	–	–	3	2	17
15	20%	33	71	–	–	1	–	16
16	all	34	32	–	–	8	1	16
17	S	(150)	22	–	–	2	–	21
18	all	11	61	–	–	1	–	1
19	S	(300)	49	–	–	5	3	16
20	all	26	105	–	–	3	4	11
22	all	1	174	–	–	–	–	1
23	S	(400)	36	–	–	5	–	23
24	all	7	13	–	–	–	1	1
25	all	2	143	–	–	–	–	1
26	S	(300)	19	11	–	–	5	2
30	10%	6	19	–	–	–	–	4
31	10%	21	52	–	–	–	–	4
32	all	16	33	–	–	1	–	3
35	all	47	58	–	–	3	18	16
36	S	(80)	51	–	–	5	–	21
37	S	(250)	31	–	–	3	6	9
38	all	58	43	–	–	1	26	21
39	S and 15%	(100)	54	–	–	–	23	7
40	all	3	242	–	–	1	–	1
41	S	(150)	33	–	–	5	11	11
42	S	(100)	?	–	–	–	17	5
43	S	(500)	53	13	–	–	1	11
45	all	6	36	–	–	–	1	2
46	all	11	51	–	–	–	10	1
47	S	(275)	79	–	–	6	–	21
49	S	(225)	?	–	–	–	28	–
50	all	37	?	–	–	–	37	–
51	S	(75)	63	–	–	2	4	16
53	all	1	78	–	–	–	–	1
54	S	(175)	?	–	–	–	25	5
58	all	30	46	–	–	–	23	7
60	S	(75)	54	–	–	–	28	2
64	S	(250)	48	–	–	–	14	13
74	all	4	103	–	–	–	–	4
75	all	4	142	–	–	–	1	3
76	S	(75)	66	–	–	9	2	17
79	all	1	55	–	–	–	1	–
85	all	11	88	–	–	–	–	8
88	all	18	137	–	–	–	1	15
91	all	46	98	–	–	–	–	23

1962) and at low tide much of the bay floor is exposed or only sparsely covered by shallow pools. The depth and salinity of the water, *per se*, are not considered to be significant factors in controlling the distribution of the Tubificidae in this study although the amount of exposure of the habitat at low tide, the degree of evaporation, and the water retention characteristics of the sediment, probably are. Such data are not available, but related sediment parameters, the mean particle size and sorting coefficient, are known for most of the bay stations. A textural analysis of the bottom sediments demonstrated that a continuous range of conditions exist in the bay, from coarse, well-sorted sands, to poorly-sorted clays which dominate the north end of the bay; a complex mosaic of intermediate sediment types occur in the central regions, and sands predominate in the bay's south end (Gorsline and Stewart, 1962). The latter authors also showed that, in general, the organic content of the sediment increased with decreasing particle size, hence it is probable that the amount of food available to oligochaetes is inversely proportional to this parameter. Therefore, the mean particle size of the sediment is thought to be a direct or indirect measurement of some factors determining tubificid distributions in this study, and will be considered in more detail below.

The numbers of each tubificid species identified from each San Quintin station (each sample $= 0.065$ m^2) and other relevant data are summarized in Table 1; for purposes of brevity, and to facilitate comparisons with other studies, mean sediment particle sizes are discussed in terms of ϕ units ($\phi = \log_2$ particle diameter in mm, hence diameters of $4 - 8 \mu = 8 \phi$, $8 - 16 \mu = 7 \phi$, $16 - 31 \mu = 6 \phi$, $31 - 62 \mu = 5 \phi$, $62 - 125 \mu = 4 \phi$, $125 - 250 \mu = 3 \phi$). From this information, and the locations of the benthic stations (Fig. 6) the distribution and density of each species can be inferred.

Abstracting and comparing pertinent data from table 1, it is evident that the three species of *Limnodriloides* bear a definite relationship to very fine sand and silt (4 to 6 ϕ optimum) in terms of both their frequency of occurrence and population size. The dominant tubificid, *L. barnardi*, occurred at 48 stations comprising all sediment classes, but was most frequently found in 4 and 5 ϕ sediments (21 percent and 40 percent of its stations respectively); maximum population density of *L. barnardi* occurred in the 4 to 6 ϕ range. *L. monothecus* occurred at 21 stations

Figure 6. Locations of benthic sampling stations in Bahia de San Quintin; redrawn from Barnard, 1962.

of which 52 percent had 5 ϕ sediments and 24 percent were 4 ϕ. However, the population density of this species was remarkably constant over its whole sediment range of 4 to 7 ϕ (about 280/m^2). Of the 28 stations occupied by *L. verrucosus*, half had sediments in the 5 ϕ class, with the remainder distributed fairly evenly over the whole sediment range of 3 to 8 ϕ; however, the abundance of *L. verrucosus* was highest in 5 to 6 ϕ and 8 ϕ substrates which may indicate that while it is capable of exploiting the finest sediments, it is partially excluded from them in this situation by competition with other deposit feeders or by the effects of predation.

The two remaining tubificids, *Tubifex postcapillatus* and *Thalassodrilus belli*, appear to be associated with the finest sediments which are located mainly at the north end of the bay. *Tubifex belli* was present in only eight samples but half of these were in the 8 ϕ class in which

the maximum abundance for this species (460/ m²) was also recorded. Only six stations were occupied by *T. postcapillatus* but three of these had 8 φ sediments. However, the species was strikingly more abundant in the 5 and 6 φ classes (about 3300 and 1700 worms/m² respectively, compared with about 250/m² in 8 φ sediments); except for the 8 φ class, these density figures were calculated from single samples whose numbers were, in turn, derived from subsamples, therefore large errors in them are possible. If the figures do reflect real trends, however, it is possible that *T. postcapillatus* has a wide sediment tolerance but is competitively restricted by *T. belli* or other detritivores in fine substrates (hence its low densities) and by *Limnodriloides* species in intermediate sediments; the latter is supported by the fact that at the 5 and 6 φ sediment stations where *T. postcapillatus* was abundant, *L. monothecus* was absent while *L. verrucosus* and *L. barnardi* were at relatively low densities.

DISCUSSION

That the distribution of freely burrowing benthic animals which feed upon their surrounding medium should be determined, in part at least, by sediment characteristics, is hardly surprising; at the extremes, a well-sorted, coarse-sand environment could be compared to rocky ground, while fine silts and clays are comparable with a rich and fertile loam. In Bahia de San Quintin, available habitats are restricted to the productive end of the scale and hence discrete communities of oligochaetes, such as those demonstrated in Cape Cod Bay, Massachusetts (Cook, 1971) cannot be delineated. However, even in the comparatively restricted sediment range of the bay, it is possible to recognize that 1) the finest silts and clay-silt are usually inhabited by *T. postcapillatus* and *T. belli* and 2) intermediate silts and fine-sands are usually exploited by *L. barnardi*, *L. monothecus*, and *L. verrucosus*. Although complicated by the differing availability of organic matter in the different substrate types, these trends support the conclusions of Bülow (1957), Brinkhurst and Kennedy (1962), Lasserre (1967), and Cook (1971) who all demonstrated that zones of differing sediments support different oligochaete faunas in the marine environment; similarly Reish (1963) found that many polychaetes in Bahia de San Quintin were associated with definite sediment types.

West coast marine oligochaetes are very poorly known; the studies by Brinkhurst and Simmons (1968) reporting on the oligochaetes, mainly Tubificidae, of the San Francisco Bay system, Tynen's (1969) description of some littoral Enchytraeidae from Vancouver Island, and the present paper, summarize existing knowledge of the class in the northeastern Pacific. Brinkhurst and Simmons (1968) found *Peloscolex gabriellae* to be the dominant oligochaete in San Pablo Bay, and south San Francisco Bay where *Peloscolex apectinatus* and *Peloscolex nerthoides* also occurred in significant numbers; these authors did not relate substrate particle size with species distributions as it was felt that the study area was uniformly available to the constituent species and that other, chemical or biological, determining factors dominated. This is undoubtedly true in some situations, and especially so in the case of polluted waters (as in San Francisco Bay). As well as increasing nutrient concentrations, many sources of organic pollution can be expected to modify bottom deposits in the direction of lowering mean particle size and hence to decrease the diversity of niches available to free-burrowing benthic organisms. Thus these results, and those of authors who report definite correlations between sediment and species distributions, are not necessarily contradictory. For example, organic enrichment or increased siltation of Bahia de San Quintin could be expected to eliminate some of the tubificids described in this paper, and from the data presented here it is possible that *L. barnardi* and *L. monothecus* could be the sensitive species; the modified distribution of the remaining three species of Tubificidae may, under these circumstances, be very difficult to relate to any sediment parameter.

Indeed these speculations lead to the conclusion that failure to detect a clear relationship between species distributions and physical sedimentary parameters may, if a diversity of sediment types are known to exist, indicate environmental deterioration.

A growing preoccupation of aquatic biologists is the concern to detect, assess and monitor sources of environmental contamination and approaches have varied from a search for indicator species to sophisticated treatments of whole systems. The success of any biological investigation, however, depends basically on accurate taxonomy; the point is stressed because this study has demonstrated that confusion between the two marine tubificids *Limnodriloides verrucosus* and *Peloscolex gabriellae* could arise if identifications

are based on superficial characteristics (papillation and setal pattern). The importance of this distinction further lies in the fact that *P. gabriellae* is resistant to high levels of organic pollution while the tolerance characteristics of *L. verrucosus* are unknown.

ACKNOWLEDGMENTS

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A NEW SPECIES OF FOSSIL *NUTTALLIA* (MOLLUSCA: BIVALVIA) FROM THE PLIOCENE OF SONOMA COUNTY, CALIFORNIA

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ABSTRACT: *Nuttallia jamesi*, new species, is described from strata assigned Pliocene age in the Sebastopol quadrangle, central Sonoma County, California. The species is similar to *N. nuttallii* (Conrad), late Miocene to Recent of California and Baja California, and to *N. olivacea* (Jay), Miocene to Recent of Japan, but differs from both in having an acuminate posterior end. The genus *Nuttallia* is restricted, in both Recent and fossil occurrence, to the north Pacific basin. It represents a temperately adapted branch of the predominantly tropical Sanguinolariinae.

Several years of field work by one of us (Guruswami-Naidu) at an exposure of soft sandstone in central Sonoma County, California, mapped as Merced Formation by Travis (1952), have resulted in a collection of more than forty marine invertebrate species (mostly mollusks) and numerous bird, fish, and mammal remains. Among the mollusks represented is a new species of the tellinacean bivalve genus *Nuttallia*, described herein. An account of the associated fauna and paleoecology will appear in a report now in preparation.

FAMILY PSAMMOBIIDAE FLEMING, 1828
SUBFAMILY SANGUINOLARIINAE GRANT AND GALE, 1931

Genus *Nuttallia* Dall, 1898

Nuttallia Dall, 1898: 58 [proposed as "section" of *Sanguinolaria* Lamarck, 1799]; Dall, 1900; Coan, 1973.

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